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Continued massive invasion of Mysidae in the Rhine and Danube river systems, with first records of the order Mysidacea (Crustacea: Malacostraca: Peracarida) for Switzerland

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Continued massive invasion of Mysidae in the Rhine and Danube river systems, with first records of the order Mysidacea (Crustacea: Malacostraca: Peracarida) for Switzerland.- A survey of invasive species belonging to the Mysidae in the Rhine and Danube Rivers and adjacent freshwater systems revealed that certain species have invaded the waters of many more countries than previously known. First records of *Hemimysis anomala* G. O. Sars, 1907 are given for Switzerland, Slovakia, Hungary, Croatia and Serbia. The same holds true for *Katamysis warpachowskyi* G. O. Sars, 1893 in Croatia and Serbia, and for *Limnomysis benedeni* Czerniavsky, 1882 in Switzerland. New or first records are also given for *L. benedeni* in the systems of artificial inland waterways of northern Germany, France and Serbia. *L. benedeni* and *H. anomala* are the first representatives of the order Mysidacea (or Mysida according to certain authors) in Switzerland. A single specimen of *Paramysis lacustris* (Czerniavsky, 1882) serves as a first record for the upper Danube in Austria. The observed spreading of *L. benedeni* in inland waterways of France suggests that it probably will soon arrive at the Mediterranean coast, with unknown consequences for indigenous populations of the closely related species in the genus *Diamysis* Czerniavsky, 1882. *H. anomala*, a top invader of continental waters in Europe, could become a potential threat at the ecosystem level if its invasion continues into large lakes, such as those connected with the Rhine system in Switzerland.

Keywords: *Hemimysis anomala* - *Limnomysis benedeni* - *Katamysis warpachowskyi* - *Paramysis lacustris* - invasive aquatic species - Ponto-Caspian invaders - continental Europe - distribution - anthropogenic dispersion - ecological impact.

INTRODUCTION

Up to the mid-20th century, only few range extensions were recorded for mysids in continental waters of Europe. Behning (1938), for example, noticed that *Paramysis ullskyi* Czerniavsky, 1882 penetrated only a few hundred kilometres into the tributaries of the Black Sea, whereas more than 3000 km into the Volga River and its tributaries. He explained the strong differences in distribution, already observed in the 1920s, by

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the more developed inland navigation along the Volga; such navigation may have favoured the dispersal of this mysid and of other peracarids attached to the fouling on ship hulls. Only few later authors adopted this view, which has recently been reconsidered by Tarasov (1996). The next major expansion event was noted in 1946 with the surprising appearance of *Limnomysis benedeni* Czerniavsky, 1882 in the winter harbour of Budapest, almost 1200 km upstream of the previously known distribution limit in the Danube River (Dudich, 1947; Woynárovich, 1955). Such a strong yet rapid displacement of the known limit suggested anthropogenic mechanisms of dispersion. Băcescu (1966) and Mordukhai-Boltovskoi (1979) already pondered why *Limnomysis* dispersed to the upper reach of the Danube, while it inhabited only the lower reach of the Volga River and only a near-mouth confluent in the Don River system.

After having been projected already in the 1930s, the next major change started in the late 1940s with the intentional introduction of mysids into hydropower reservoirs, lakes, and other water bodies in order to enrich the supply of food for fish. From 1948-1965 more than one hundred million mysids, together with a great variety of other invertebrates, were intentionally released into more than 200 water bodies of the former Soviet Union. Our knowledge about these introductions and their outcomes is quite obscure. This is mainly due to the inaccessibility of cryptic literature (citations in Komarova, 1991; Grigorovich *et al.*, 2002) and inadvertent stocking (Pligin & Yemel'yanova, 1989).

During the next decades some of the mysid species showed local secondary spreading from the introduction sites; a few species – essentially the four presented in Fig. 1 – transgressed the large continental watersheds and invaded vast areas of central, northern and western Europe. In the early 1980s it became clear that mysid introductions could have adverse effects at the ecosystem level (Rieman & Falter, 1981; Fürst *et al.*, 1984; Ketelaars *et al.*, 1999), and most of the intentional introductions were stopped. This had no direct effect on the ongoing non-intentional mechanisms of dispersion, which culminated in 1997-1998 with the explosive range expansion of *Hemimysis anomala* G. O. Sars, 1907 and *L. benedeni* in waters of the Rhine system. The present contribution indicates further range expansions of these and additional species in large areas of continental Europe, for the first time also including Switzerland. A critical analysis of invasion histories could help to estimate the potential for future dispersal and possible threats to ecosystems and biodiversity.

MATERIAL AND METHODS

By convention, the river kilometres are numbered in downstream order for the Rhine and its tributaries, but in upstream order for the Danube. Measurements of abiotic parameters were taken as explained in Wittmann (2002). Salinity was calculated from conductivity measurements corrected to 25°C, as a dimensionless equivalent of overall ionic content rather than content of sea salts. Mass occurrence was defined as ≥1000 specimens and, as an additional prerequisite, ≥10 times the average yield of positive samples taken with the same method under comparable conditions.

The diverse sampling methods follow those outlined in Wittmann (2002), with the exception of the following modifications introduced in 2004: the hand nets were optionally attached to a 4.6 m telescopic rod, allowing for sampling from the shore down to 3.5 m depth; the drift net was larger (opening 2872 cm^2, mesh size 500 μm for the anterior 150 cm of length, and 280 μm for the posterior 100 cm) than before and kept in position 10 cm above the substrate by a steel cage. Ten bottle traps were used in 2005, designed essentially according to Odenwald *et al.* (2005); the main difference was that the bottles were tightly attached to 0.5 kg weights in order to throw them, filled with about 1.5 l of water and the bait, several metres from the shore. The bait was commercial tablets for aquarist use («Wels Tabs mit Spirulina» by 'Fa. Product Aquaristik-Terraristik' in Austria, imported from 'Hicari Corp.' in Japan), composed of dried, compressed algae, insects and crustaceans.

The yield obtained with the baited traps confirmed the findings of Odenwald *et al.* (2005) that *Hemimysis anomala* is more effectively trapped than other mysid species (*Limnomysis benedeni* and *Katamysis warpachowskyi* G. O. Sars, 1893). The drift net was useful for currents >0.2 m/s, especially if no or only few stagnant side arms were accessible in a particular river stretch. Drift samples yielded all three above-mentioned species more often than the remaining methods. Drift nets and bottle traps were set up over night.

In 1985-2001 a total of 390 samples containing mysids were taken along the Rhine and Danube Rivers, from the upper reaches down to the deltas, as well as along the coasts of Romania and western Turkey (Black, Marmora, Aegean Seas) and in adjacent freshwaters. Part of these sampling data is available in Wittmann (1995, 2002), Wittmann *et al.* (1999) and Wittmann & Ariani (2000). In 2002-2005 a total of 230 samples were taken at 117 stations in the Rhine and Danube systems and in adjacent waters.

Additional data were obtained from hand net samples taken by B. Csányi during the Cousteau-Expedition 1991 at 50 stations between Danube-km 2786 and km 80. Twelve of these samples contained mysid species. Two samples with *L. benedeni* were studied in the collection of the Biologija Univerza Ljubljana: from the Tisa River in Serbia (26 June 1977, leg. I. B. Sket) and from the Danube at Donji Milanovac in the Carpathian breakthrough (8 Oct. 1984). Ten samples with *L. benedeni* and *Diamysis pengoi* (Czerniavsky, 1882), taken on 21 Aug.-30 Sept. 1924 by V. Pietschmann and O. Koller at Lake Patiu (46.20°N, 28.0167°E, at the River Prut, an affluent of the Danube at km 133) and at six stations from Danube-km 181 down to km 19 of the Chilia branch, were studied in the collection of the Naturhistorisches Museum Wien (Crust. Coll. nos. 5960, 5962, 13397-13408).

In 1985-2004 most of the material was fixed in a solution of 4% formalin in ambient water and later transferred into an aqueous solution of 60% ethanol with 10% diethylene glycol. In 2005 most material was fixed in 96% ethanol in view of future genetic studies. Representative material was deposited in the Muséum d'histoire naturelle de la Ville de Genève and the Naturhistorisches Museum Wien (Crust. Coll. nos. 20685-20704).

RESULTS

Hemimysis anomala G. O. Sars, 1907 Figs 1A, 2

The sampling campaigns in 2004-2005 yielded this species at 19 stations. These are shown in Fig. 2 together with published data from previous campaigns and litera-

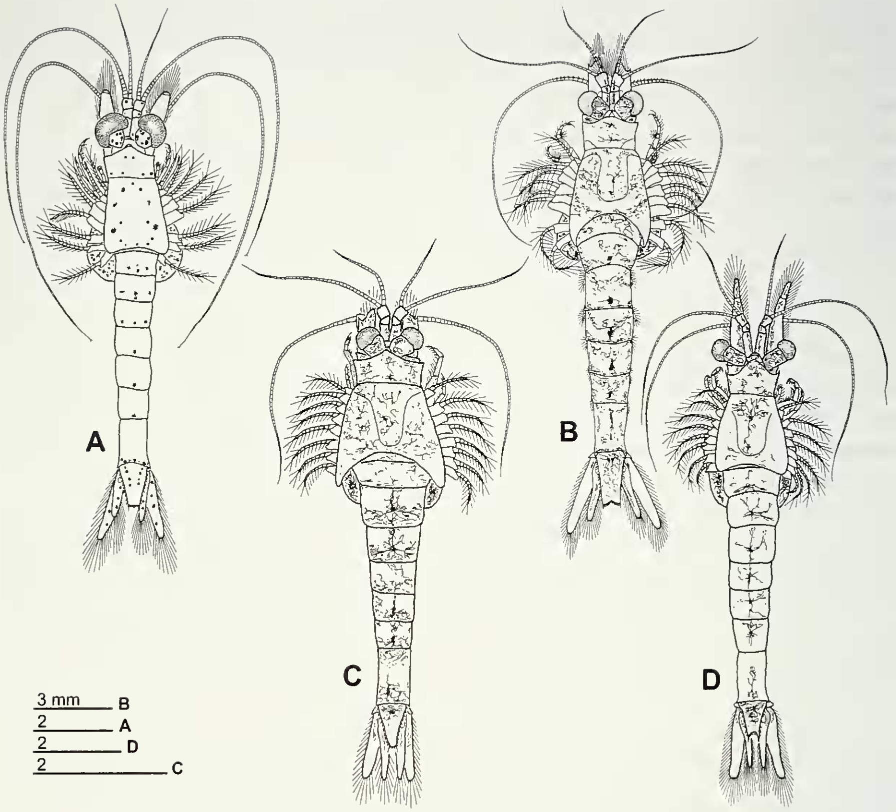

FIG. 1

The currently most expansive mysid species in continental waters of Europe: *Hemimysis anomala* (A), *Paramysis lacustris* (B), *Katamysis warpachowskyi* (C) and *Limnomysis benedeni* (D). Adult females from the Danube River in Vienna (A, C, D) and from the Danube Delta (B). Adults of the four species are macroscopically distinguished by body proportions, and by the size and form of eyestalks and cornea. A, C and D taken from slightly schematized drawings in Wittmann (2002).

ture data. A number of first records were noted in 2005: *H. anomala* was found southwards of the already published range limit in the Rhine system, namely in Strasbourg (km 295) and Basel (km 170). The finding at Strasbourg is represented by a total of seven specimens trapped in five out of seven bottles exposed over night (24/25 Oct. 2005) on the right river bank, in the Port de la Redonne and at the main harbour entrance (48.59372°N, 7.80210°E). The new southern limit of *H. anomala* in the Rhine system is now marked by the harbour of Kleinhüningen (km 170), where a total of five specimens were found in three out of six baited bottle traps exposed over night (47.58757°N, 7.59340°E; 25/26 Oct. 2005; first record for Switzerland). A single specimen of *H. anomala*, trapped at Danube-km 1865 at the entrance of the dock harbour of Bratislava, represents the first record of this species for Slovakia (48.12443°N, 17.15068°E; 16 Sept. 2005). A number of new records fill the large gap along the middle course of the Danube River: the first record for Hungary was taken at the right river bank at km 1578 in Dunaújváros, where 40 specimens were collected by drift net (46.95704°N, 18.95602°E; 28/29 July 2005). A single specimen of *H. anomala* collected by drift net at the right river bank at Danube-km 1333 in Vukovar represents the first record for Croatia (45.35380°N, 19.00383°E; 29/30 July 2005). The first record for Serbia was taken at the right river bank at km 1059 in the impoundment basin in Veliko Gradište, where 1349 specimens were collected by drift net (44.76710°N, 21.51488°E; 30/31 July 2005). This station lies 19 km above the entrance into the Carpathian breakthrough of the river.

Mass occurrences were found at certain stations in turbid waters with varying ionic content, i.e. in the impoundment basin (371 μS/cm) of the Danube River at km 1059 (14 days after the peak of a moderate flood event), in the Mittellandkanal (km 4) at 1600-1630 μS/cm and in the winter harbour of Linz (Danube-km 2132) at 296 μS/cm. Remarkably, the first two of these three stations simultaneously showed a mass occurrence of *Limnomysis benedeni* (see below). The *H. anomala* mass occurrences in the Mittellandkanal and at Linz were local. Inspections of the same Linz harbour site, this time operating the same hand net from a swimming platform in the same way, yielded no *Hemimysis* on 18 June 2004, 1167 specimens on 15 July 2005 and again zero on 14 Aug. 2005. The rich yield was made three days after the peak of a strong flood event, the zero yields during periods of normal water levels. *L. benedeni* collected together with *H. anomala* with the same nets showed a completely different phenology: 16, 294, and 652 specimens, respectively.

In 2004-2005 *H. anomala* was found only in strongly anthropogenic habitats. The measurements of abiotic factors are integrated in Table I. The 19 positive sampling stations showed massive structures for shore or river bank stabilization, such as large stones, boulders, concrete or steel. Additional structures included vegetation, such as algal cover on hard substrate or loose stands of submerged macrophytes. Hand net samples taken during the day contained *Hemimysis* at only six stations where the animals were found between large stones or boulders in ≤1.5 m depth (≤3.5 m examined). A slightly higher abundance in shallow water was revealed by 36 positive bottle traps exposed over night at ten stations in 0.6-3.5 m depth.

Limnomysis benedeni Czerniavsky, 1882 Figs 1D, 2

The records of this species yielded by the Cousteau-Expedition 1991 and own excursions in 1985-2005 in the Rhine and Danube systems, and in waters of western Turkey, are given in Fig. 2, together with available literature data. The Cousteau-Expedition captured this species on the banks of the Danube River at kms 2112, 1533, 1070, 954, 877, 851, 624, 506, 496 and 296. Own sampling in 2004-05 yielded this species at 92 stations. The following first records were taken in 2005: the species was found southwards of the already published range limit on the Rhine River and in its parallel, artificial side arm Grand Canal d'Alsace, at four stations between Breisach (km 225) and Basel (km 170). Hand net collecting in the harbour of Kleinhüningen in Basel (47.58740°N, 7.59142°E) yielded the first record of the order Mysidacea for Switzerland. Hundreds of *Limnomysis* specimens were found there during two inspections (10 July and 26 Oct. 2005), with maximum densities in 0.2-1.0 m depth among

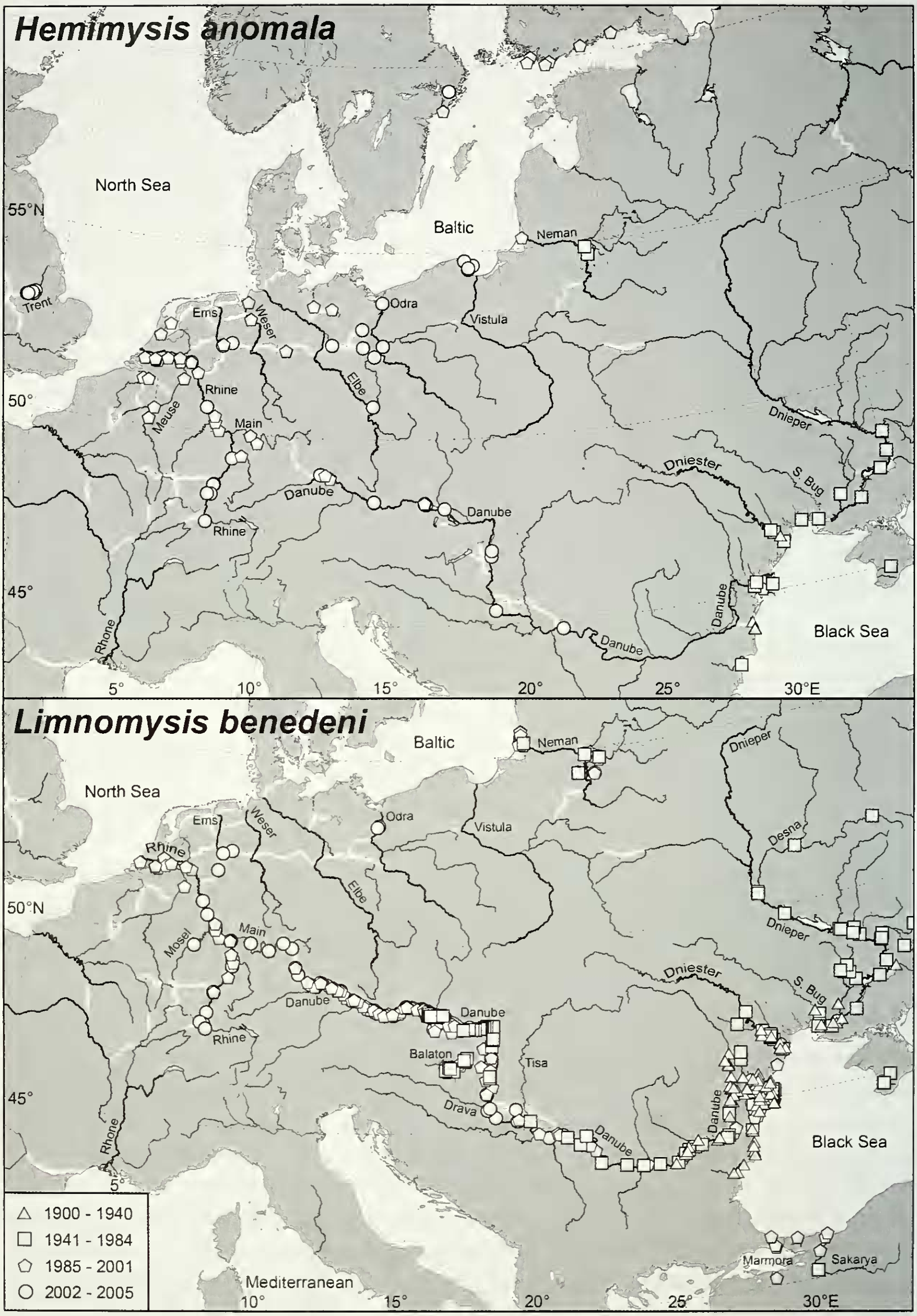

FIG. 2

Distribution of *Hemimysis anomala* and *Limnomysis benedeni* in the Rhine-Danube system and other waters. Overlapping symbols are arranged with the older records on top, so that the

the filiform, green algae covering vertical concrete and steel walls. Eight stations further upstream in the river and in Lake Constance (Bodensee) contained no mysids. Also, a westward range expansion in and from the Rhine system was noted by findings in the Mosel River at Riol (49.79697°N, 6.79727°E), Canal de la Marne au Rhin at Strasbourg (48.59133°N, 7.78302°E), Canal du Rhône au Rhin at Niffer (47.71270°N, 7.50190°E) and at Mulhouse (47.75442°N, 7.34880°E). *L. benedeni* was found for the first time in navigation channels of NW Germany: Mittellandkanal at km 4 and km 35, and Dortmund-Ems-Kanal at km 48. The only mysid species found in the Ems-Jade-Kanal was the marine euryhaline species *Praunus flexuosus* (O. F. Müller) in the brackish reach (S = 26-31) at km 70-71. Regarding the Danube system, first records of *L. benedeni* are here given for the Drava River at km 20 in Croatia, for the Tisa River 9 km above mouth into the Danube River (collection material from 1977) in Serbia, and for the DTD-Channel-System that connects (among others) the Tisa and Danube in Serbia (record in the Veliki Kanal at Srbobran, 45.54040°N, 19.78738°E).

Mass occurrences were found at certain stations in turbid waters with varying ionic content, i.e. in the Mittellandkanal (km 4) at 1600-1630 μS/cm, in the Neusiedler See at 3580 μS/cm, in Lake Balaton (811 μS/cm) and in the impoundment basin (351-371 μS/cm) of the Danube River at km 1059 (14 days after the peak of a moderate flood event). The first three of these mass occurrences were local, while the impoundment basin was not tested in this regard.

In 2004-2005 *L. benedeni* was found in a broad range of habitats from near-natural to strongly anthropogenic. The measurements of abiotic factors are integrated in Table I. Maximum densities of *Limnomysis* were observed among vegetation, with a preference for stands in only 0.3-1.0 m depth; nonetheless, *L. benedeni* was also present down to the greatest depth sampled (4 m). Very high densities were found among brush-like plant structures, such as cover of long, filiform algae on hard substrates or fine roots of *Salix* trees, or in dense stands of submerged macrophytes or in flooded terrestrial weeds. Densities were generally lower on and in the space between stones and over soft substrate. A few animals even lived on bare walls of wood, concrete or steel. As observed by snorkelling during the day, the animals swam a few cm from the substrate or were in direct contact with it. Hand net collecting and horizontal surface tows from boats showed that part of the population kept a greater distance from the substrate during the night, with a few specimens swimming up to the surface.

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expansion history can be traced from the symbols indicating different periods. White lines indicate man-made canals, black lines rivers. Original records (in part covered by superimposed symbols) are from waters of the Rhine-Danube system, channel systems in France and northwestern Germany, and from waters of western Turkey. Literature records are from Salemaa and Hietalahti (1993), Eggers *et al.* (1999), Kelleher *et al.* (1999), Wittmann *et al.* (1999), Tittizer *et al.* (2000), Borcherding (2001), Haesloop (2001), Grigorovich *et al.* (2002), Rehage & Terlutter (2002), Wittmann (2002), Zettler (2002), Rudolph & Zettler (2003), Lundberg & Svensson (2004), Arbaciauskas (2005), Horecký *et al.* (2005), Janas & Wysocki (2005), Michels (2005), Müller *et al.* (2005), Dumont (2006), Holdich *et al.* (2006) and additional literature cited in these publications.

Katamysis warpachowskyi G. O. Sars, 1893 Figs 1C, 3

The sampling campaigns in 2004-2005 yielded this species at 21 stations. These are given in Fig. 3 together with published data from previous campaigns and literature data. This species was found only in the Danube system, where the following new records were noted: on 16 June 2004, one adult female was taken with hand net close to the fish-ladders, immediately below the impoundment weir of Greifenstein (48.3495°N, 16.2465°E) at river-km 1949 in Austria. This finding shifted the known distributional limit of *K. warpachowskyi* by only 13 km further upstream. This was within the same impoundment basin in which the species had already been detected three years earlier (Wittmann, 2002). A number of new records fill the large gap along most of the middle course of the Danube: the first record for Croatia was nine specimens of *K. warpachowskyi* sampled by hand net in the yachting harbour of Vukovar at river-km 1333 (45.35313°N, 19.00408°E; 29 July 2005). The first records for Serbia were one specimen taken with the hand net at the right river bank near Veliko Golubinje (44.46675°N, 22.17268°E) in the Carpathian breakthrough at km 986, followed by eight specimens taken with the drift net in the impoundment basin at Veliko Gradište at km 1059, and then 46 specimens with the hand net in the winter harbour of Kovin at km 1109 (all three samples on 30/31 July 2005).

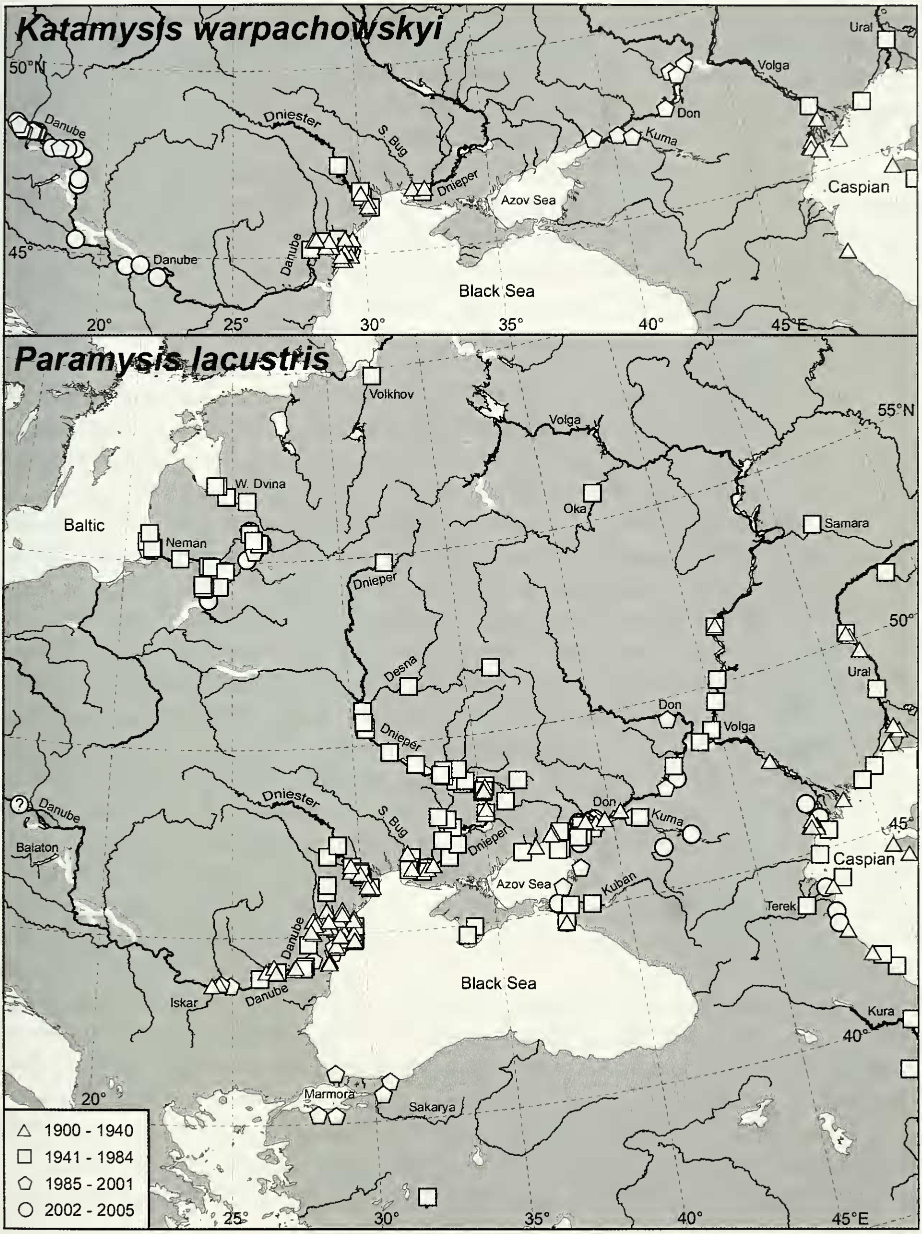
In 2004-2005 *K. warpachowskyi* was found in a broad range of habitats from near-natural to strongly anthropogenic. The measurements of abiotic factors are integrated in Table I. Maximum densities of *Katamysis* were observed on boulders, large stones and on coarse to soft substrates with plant debris, with a preference for stands in ≥1.5 m depth, but also present in 0.2-1.5 m. This species was also found between submerged macrophytes, between flooded terrestrial weeds and in accumulations of stones and shells. In most hand net samples, *K. warpachowskyi* occurred together with *Limnomysis benedeni* and the snail *Viviparus acerosus* (Bourguignat, 1862). Generally, the drift net and bottle traps yielded only small numbers of *Katamysis*. No mass occurrences were recorded for this species.

Paramysis spp. Figs 1B, 3

The records of *P. lacustris* (Czerniavsky, 1882) yielded by the Cousteau-Expedition 1991 and by own excursions in 1985-2005, in the Danube system, are given in Fig. 3, together with available literature data. The Cousteau-Expedition collected *Paramysis* species only in the lower reach of the Danube River. A total of 13 specimens of *P. lacustris* were taken at km 624, km 595, km 489 and km 296. Only fragments of two individuals of *P. intermedia* Czerniavsky, 1882 were sampled at km 624 and km 595. The sampling campaigns of 1985-1998 yielded *P. lacustris* in the Predelta (Lake Sinoe), in the main river branches of the Danube and in a great number of lakes, side arms and canals of the Danube Delta (325-3020 μS/cm). The excursion to western

FIG. 3

Distribution of *Katamysis warpachowskyi* and *Paramysis lacustris* in the tributary system of the Black Sea and other waters. Overlapping symbols are arranged with the older records on top, so that the expansion history can be traced from the symbols indicating different periods. White



lines indicate man-made canals, black lines rivers. Original records (in part covered by superimposed symbols) are from waters of the Danube system and of western Turkey. Literature records are from Băcescu (1940, 1954), Mordukhai-Boltovskoi (1964, 1979), Pligin and Yemel'yanova (1989), Komarova (1991), Tarasov (1996), Daneliya (2001, 2003), Arbaciauskas (2002), Grigorovich *et al.* (2002), Wittmann (2002), Gruszka *et al.* (2003), Audzijonyte (2006) and additional literature cited in these publications.

Turkey in July 1988 showed the presence of this species in a total of five lakes (Fig. 3) near the coasts of the Marmora Sea (Uluabat Gölü, Kus Gölü) and the Black Sea (Durusu Gölü, Sapanca Gölü, Akgöl). All these lakes contained clearly freshwater in the conductivity range of 270-500 μS/cm at surface temperatures of 27-30°C. One immature female of *P. lacustris* surprisingly appeared in a hand net sample taken by snorkelling in stands of *Myriophyllum* in 1.5 m depth in the almost isolated (see 'Discussion') backwater Alte Donau in Vienna (at height of Danube-km 1930; 48.24213°N, 16.42132°E; 10 June 2004). Despite great efforts, no further specimens belonging to this species could be found in waters along the upper and middle reaches of the Danube in 2004-2005.

DISCUSSION

Range expansion history of *Hemimysis anomala*: This species has populated vast areas of continental Europe, originating from an exclusively Ponto-Caspian range in the early 20th century. Indigenous populations were found in the salinity range of 0-18 (Table I), living over hard substrate or algal vegetation along the shores of the Caspian Lake, and the Black and Azov Seas. Before human interventions, the species was known as an essentially estuarine or 'marine' (in terms of NW Black Sea salinities) animal, penetrating not more than 40-60 km into the lower reaches of rivers. Băcescu *et al.* (1971) pointed it out as the only mysid species of Caspian origin occurring in the open Black Sea. Before 1998 the records of *H. anomala* in the Danubian range were restricted to the delta up to 34 km distance from the Black Sea (Băcescu, 1954; Popescu, 1963; most later records are merely citations of these two papers). This was essentially confirmed by own sampling in the delta, where *H. anomala* was rare and only taken in 1995 at mile 13.6 of the Sulina branch, and in 1998 at km 68 of the Sfintu Gheorghe branch (Wittmann *et al.*, 1999). Due to artificial deepening of the Sulina branch, a distinct influence of saline waters invading up to km 80 inland from the sea were reported during the drought season in August-September (Bondar, 1983). Thus the 'original' Danubian range of this species fitted well to the distribution of an essentially estuarine species (Băcescu, 1954) that only marginally penetrates into freshwater.

H. anomala started its range expansion in 1957 as an invader of European brackish and freshwaters by intentional introduction into an impoundment basin of the Dnieper River in the course of fisheries management (Pligin & Yemel'yanova, 1989). The main aim was that this photophobic species would enrich the spectrum of fish food in deep impoundment basins. This actually worked: *Hemimysis* established populations in up to 20-50 m depth (Zhuravel, 1960). This approach was pursued in other reservoirs and lakes of the former Soviet Union (Grigorovich *et al.*, 2002). From impoundment basins in tributaries of the Baltic Sea the species spread into brackish coastal waters of Lithuania, Finland, Sweden and Poland (Razinkovas, 1996; Arbaciauskas, 2002; Lundberg & Svensson, 2004; Janas & Wysocki, 2005). From there it invaded more western Baltic tributaries, together with the River Odra (Gruszka *et al.*, 2003), the system of navigation channels in northern Germany (Eggers *et al.*, 1999; Rehage & Terlutter, 2002; Zettler, 2002; Rudolph & Zettler, 2003; Müller *et al.*, 2005) and, again westwards, tributaries of the North Sea (Elbe and Weser systems; Haesloop, 2001; Horecký *et al.*, 2005). Additional, so far unpublished records from waters connected with the channel system in north-eastern Germany were kindly communicated by E. Rudolph (Havel): Spree River at the village of Radinkendorf, 52.21133°N, 14.27235°E, 24 Dec. 2004, leg. Wulf (Lamitsch), and Havel River at the village of Bahnitz, 52.49717°N, 12.40410°E, 2 Sept. and 1 Nov. 2005, leg. Rudolph.

In 1997-1998 *H. anomala* showed an explosive range expansion by appearing in vast areas of the Rhine-Main-Danube system, ranging from brackish and freshwaters in the Rhine Delta, to the middle Rhine, the rivers Main and Neckar, and the upper Danube. Already in 1999 this species was reported in the Westerschelde estuary in Belgium (Verslycke *et al.*, 2000). Shortly thereafter, in 2000, it appeared at two stations in the middle reach of the Meuse River (Usseglio-Polatera & Beisel, 2003). In June 2005 (four months before my findings reported above) it appeared for the first time in the north-east of France (Dumont, 2006). Due to an unknown introduction, the species surprisingly appeared in 2005 in waters of the Trent River in the English Midlands (Holdich *et al.*, 2006).

Even if certain populations may have been overlooked in earlier years, the speed of range expansion clearly points to anthropogenic dispersion by navigation, as also pointed out below for *Limnomysis benedeni*. The extent and speed of the invasions by both species were probably favoured by the opening of the Main-Danube-Channel in 1992. From the currently available data for *H. anomala* one cannot definitely conclude whether the invaders of 1997-1998 originated from Baltic populations and transgressed this channel from north to south, or if they came from the Black Sea (Danube Delta) and transgressed the channel from south to north (see discussions in Kelleher *et al.*, 1999; Wittmann *et al.*, 1999; Bij de Vaate *et al.*, 2002; Müller *et al.*, 2005). Multiple immigrations cannot be excluded (Müller *et al.*, 2005). Future genetic studies could be helpful to clarify such questions.

With the anthropogenic appearance in the upper Danube in 1998 (Wittmann *et al.*, 1999) a very large gap of records between km 1933 and km 68 became obvious, covering the entire middle and the lower reaches of the river, and part of the delta. A total of 37 hand net and drift net samples taken by me in 2001-2004 at 20 stations between km 1931 and km 1722 yielded *Hemimysis* only at km 1931. In accordance with this, Košel *et al.* (2003) reported only *L. benedeni* and *Katamysis warpachowskyi* but no *H. anomala* for the fauna of Slovakia. Possibly there was a disjunction in the Danubian distribution of *H. anomala* over a few years. A substantial part of the gap was closed in 2005 by the above-presented first records for Slovakia, Hungary, Croatia and Serbia. As in *L. benedeni*, a further upstream (southwards) expansion was noted in 2005 when *H. anomala* was recorded from the French (Dumont, 2006) and the Swiss reach of the Rhine for the first time. Most of these findings were made in harbours, pointing to a possible anthropogenic dispersion by navigation.

The present paper is the first to demonstrate the mass occurrence of *H. anomala* in rivers. The first hypothesis is that these mass occurrences were local and short-lived, possibly caused by flood events that had displaced the mysids by passive drift and/or by active avoidance of strong currents, so that the animals accumulated in more calm zones (harbour at Danube-km 2132, or deep and wide impoundment basin at km 1059). This will be the subject of future research.

RANGE EXPANSION HISTORY OF *LIMNOMYSIS BENEDENI*: As in the preceding species, *L. benedeni* also populated vast areas in continental Europe, starting from an essentially Ponto-Caspian distribution in the early 20th century. Indigenous populations were found in the salinity range of 0-14 (Ovčarenko *et al.*, 2006; Table I), with the greatest population densities in the oligohaline range (0.5-5), but the greatest number of populations in freshwater. Mass occurrences were only found at pH > 7.7. A favourable development in alkaline waters is also indicated by findings of Szalontai *et al.* (2003) that the oxygen consumption of juvenile *Limnomysis* is lower at pH 8.4 than at pH 5.4. The animals mainly dwelled among vegetation in stagnant and slow-flowing waters in the tributary systems of the Caspian Lake and the Black and Azov Seas. Own sampling in July 1988 revealed several populations in streams and lakes belonging to the drainage systems of the Marmora Sea and the Black Sea in western Turkey (Fig. 2). In most large Ponto-Caspian river systems this species penetrated several hundred kilometres beyond the oligohaline reach of the mouth area. The Danubian distribution once extended from the saline mixing zone in the Black Sea up to river-km 460. In any case, the primary distribution did not extend into the former cataract stretch between km 941 and km 1040 in the Carpathian breakthrough.

L. benedeni started its range expansion as an invader of European freshwaters in 1946, when it surprisingly appeared in the winter harbour of Budapest at Danube-km 1644 (the erroneous indication in Dudich, 1947: Tab. 1, was corrected by Woynárovich, 1955; now there is a bridge at this point, today's harbour entrance is at km 1642). During the following five decades *L. benedeni* expanded its distribution in the Danube upstream to the beginning of the Main-Danube-Channel at Kelheim in a series of small (1-173 km) steps. By incorporating additional literature and data from collections, the list given by Wittmann *et al.* (1999) is here updated. Fourteen stations are currently known: km 1683 (year 1949), km 1787 (<1953), km ≈1872 (<1954), km 1911 (1973), km 1919 (1982), km 1920 (1983), km 2093 (1986), km 2112 (1991), km 2132 (1992), km 2214 (1993), km 2228 (1994), km ≈2320 (1995), km 2376 (1997), km 2410 (1998). *Limnomysis* transgressed the Main-Danube-Channel probably shortly before 1997 and thereafter colonized vast areas of the Rhine system, probably in downstream direction, in about 1997-1998. Already in 1998 a further upstream (southwards) expansion was noted by the appearance of *Limnomysis* in the French reach of the Rhine (Wittmann & Ariani, 2000). Most of the observed upstream expansions probably reflect passive transport by ships. Specimens of this species were found on the outside hull of ships, and also inside, particularly in rest water (bilge water) and in cooling-water filters (Reinhold & Tittizer, 1998; Wittmann *et al.*, 1999; Bij de Vaate *et al.*, 2002). The new records, presented above for the Mosel River, the upper Rhine and the navigation channels in France, all came from navigable courses and therefore potentially reflect passive transport by navigation.

L. benedeni was intentionally introduced mainly in the 1950-1960s in eastern Europe, in order to enrich the supply of food for fish. These operations started in 1948 with the release of mysids into a hydropower reservoir of the Dnieper River, followed during the next decades by a great number of other waters in the former Soviet Union (Grigorovich *et al.*, 2002), particularly in Lithuania (Arbaciauskas, 2002), and in Hungary (Lake Balaton; Woynárovich, 1955). Introduction of *Limnomysis* into Lake

Aral (Kazakhstan and Uzbekistan; Mordukhai-Boltovskoi, 1979) was possibly due to inadvertent stocking (Aladin *et al.*, 2003). From introduction sites along tributaries of the Baltic Sea *L. benedeni* spread into coastal waters (Olenin & Leppäkoski, 1999; Arbaciauskas, 2002) and other tributaries, including the waters of the Odra system in Poland (Michels, 2005). The new records presented above for navigation channels in north-western Germany may originate from a (north-) eastwards expansion of populations from the Rhine system, although a westwards expansion from Baltic tributaries appears possible as well.

RANGE EXPANSION HISTORY OF *KATAMYSIS WARPACHOWSKYI*: In most large Ponto-Caspian river systems *Katamysis* originally penetrated up to 200 km into rivers of the Black Sea, or 120 km into those of the Caspian Lake. Black Sea populations were found in a salinity range of only 0-5, with the optimum in freshwater; Caspian populations showed a broader range (0-14; Table I). A similar difference was also observed in *Paramysis lacustris* (Table I). In 2000 *K. warpachowskyi* surprisingly appeared in waters of the Don system (Fig. 3), from where it had never been reported before. According to Daneliya (2001), this may indicate a recent immigration from the Volga River via the Volga-Don navigation channel, which was completed in 1951-1952. Deliberate introductions were of little importance for the distribution of this species. In 1956 it was released into the Dubossary reservoir (Dediu, 1966), upstream of its previously known distribution range in the Dniester River. For more details on the distribution, ecology, bionomics and possible modes of dispersion of *K. warpachowskyi*, see Wittmann (2002).

In 2001 this species was surprisingly detected at km 1936, more than 1700 km upstream of its previously known limit of distribution in the Danube (Wittmann, 2002). So far it has not transgressed the limits of the watersheds belonging to its exclusively Ponto-Caspian range. With the new record at km 1949 in 2004 the upper limit shifted by only 13 km and thus remained within the same impoundment basin. This was not surprising, because the comparatively rheophilic *K. warpachowskyi* is considered to be capable of swimming against the water currents observed along the banks of this impoundment basin under normal hydrological conditions.

Within the same month (Oct. 2001) an already differentiated distribution was found along the Austrian, Slovakian and Hungarian reach, down to km 1769 (Wittmann, 2002). This campaign was continued in 2004 with sampling down to Danube-km 1722, in the side arm Kis Duna (47.76335°N, 18.69988°E; 23 June 2004) near its flow back into the main river, and in 2005 down to km 986 in the Carpathian breakthrough, yielding the first records for Croatia and Serbia. In no case was a lower limit documented by negative downstream samples, because the species was always present at the lowest station examined. Extrapolating this, it seems likely that before 2005 a continuous population range already existed from kms 1936-1949 down to the delta. The absence of this species in samples taken at 26 stations in the Hungarian and Austrian reach in 1997-1998, as well as in samples of preceding campaigns (Nesemann *et al.* 1995; Wittmann, 1995), including the Cousteau-Expedition 1991, suggest that the middle and upper reaches of the Danube were colonized within a few years before 2001.

TABLE I. Hydrological and physicochemical parameters at sampling stations of four Ponto-Caspian mysid species[a].

Samples selected / parameter	*Hemimysis anomala* m ± S.D.[b]	range	n	*Limnomysis benedeni* m ± S.D.[b]	range	n
All samples:						
Depth (m)	4.037 ± 5.422	0-60	103	1.452 ± 1.166	0-10	479
Water current (m/s)	0.152 ± 0.222	0.0-0.81	98	0.106 ± 0.194	0.0-1.5	443
Temperature (°C)	17.21 ± 4.47	2-28	78	19.38 ± 4.79	0-31	353
Salinity	2.140 ± 4.209	0.1-18.0	87	0.594 ± 1.659	0.0-14.0	345
Conductivity (μS/cm)	3792 ± 6947	279-29200	87	1215 ± 2774	195-22300	345
pH	7.866 ± 0.503	6.35-8.65	63	7.970 ± 0.599	5.54-9.57	267
Carbonate hardness (°d)	8.642 ± 0.975	6-12	60	9.209 ± 3.455	3-30	191
Oxygen content (mg/l)	7.197 ± 1.422	3.99-10.80	63	7.922 ± 1.994	3.75-18.10	263
Turbidity (NTU)[c]	28.61 ± 26.29	5-137	63	34.17 ± 41.44	1-274	266
All regions, drift samples excluded:						
Water current (m/s)	0.031 ± 0.078	0.0-0.35	69	0.073 ± 0.148	0.0-1.0	406
All sample types, samples in the Caspian Lake excluded:						
Salinity	1.475 ± 3.317	0.1-18.0	82	0.480 ± 1.274	0.0-14.0	340
Conductivity (μS/cm)	2697 ± 5486	279-29200	82	1025 ± 2139	195-22300	340

Samples selected / parameter	*Katamysis warpachowskyi* m ± S.D.[b]	range	n	*Paramysis lacustris* m ± S.D.[b]	range	n
All samples:						
Depth (m)	2.011 ± 1.570	0-10	84	3.908 ± 4.896	0-48	122
Water current (m/s)	0.146 ± 0.283	0.0-1.5	74	0.061 ± 0.122	0.0-0.5	83
Temperature (°C)	17.72 ± 4.61	0-27	77	19.82 ± 5.54	0-30	70
Salinity	0.919 ± 2.915	0.1-13.8	74	1.909 ± 3.269	0.0-13.8	82
Conductivity (μS/cm)	1738 ± 4828	279-22873	74	3451 ± 5450	270-22873	82
pH	7.693 ± 0.729	6.13-9.35	54	8.344 ± 0.625	7.42-9.42	24
Carbonate hardness (°d)	9.294 ± 3.437	5-25	51	9.889 ± 2.374	8-16	18
Oxygen content (mg/l)	8.359 ± 1.972	3.99-16.99	54	7.401 ± 1.979	5.01-12.17	23
Turbidity (NTU)[c]	30.02 ± 42.81	1-272	54	43.30 ± 49.97	1-194	23
All regions, drift samples excluded:						
Water current (m/s)	0.122 ± 0.282	0.0-1.5	67	0.051 ± 0.109	0.0-0.5	80
All sample types, samples in the Caspian Lake excluded:						
Salinity	0.159 ± 0.413	0.1-5.0	68	1.179 ± 1.956	0.0-8.0	75
Conductivity (μS/cm)	475 ± 721	279-8800	68	2242 ± 3338	270-13800	75

[a] data sources as in Figs 1, 2

[b] mean ± standard deviation

[c] nephelometric turbidity units

RANGE EXPANSION HISTORY OF *PARAMYSIS* SPP.: In the large Ponto-Caspian river systems *P. lacustris* originally penetrated about 200-600 km into the Danube, Dnieper, Don and Ural Rivers, and about 900 km into the Volga. Almost the same penetration distances were found for *P. intermedia*, with the remarkable difference that it reached as far as about 2000 km from the Caspian Lake into the Kama River, a northern tributary of the Volga. In the Caspian Lake *P. lacustris* showed a more continuous distribution in estuarine waters to freshwaters along the west coast (Fig. 3), while the distribution in the more saline Black Sea showed a distinct maximum at coastal stretches influenced by the freshwater input of large rivers. As shown in the 'Results', *P. lacustris* was found in freshwater lakes of western Turkey, where it locally occurs together with *Limnomysis benedeni* (Figs 2, 3). It is remarkable that *P. lacustris* was also found in Lake Beizehir (Băcescu 1948, 1966) in the Anatolian highland. The salinity range of *P. lacustris* was 0-14 (Table I); the range was 0-12 for *P. intermedia*.

In 1936 the upper limit of the known distribution of *P. lacustris* and *P. intermedia* in the Danube system was in the Orlea swamps (Lake Potelu) that drain into the river at km 644 (Băcescu, 1940). In 1991 this limit again coincided for both species and was still close to the previous position, downstream of the mouth of the Iskar River at km 624, as derived from the material of the Cousteau-Expedition.

In 2004 the single specimen of *P. lacustris* (see 'Results') surprisingly was recorded at the height of Danube-km 1930 in an almost isolated backwater. This backwater is connected with an artificial side arm of the river solely by an underground pipe and pumping station for stabilization of the water level. This was 1286 km upstream from the nearest documented population (Lake Potelu), or 620 km upstream from the nearest confluence with the drainage system of an introduction site (Lake Balaton). Due to its relatively isolated position, this single specimen does not provide definite evidence of a viable population of *P. lacustris* unless further material is found, and is therefore indicated with a question mark in Fig. 3. This species, along with *P. intermedia*, already had disappointed previous expectations of existing populations: according to Băcescu (1966 and pers. comm.) and Băcescu *et al.* (1971), *Paramysis* stocks were taken from Lake Olţina (drainage into Danube at km 338) and transplanted into Lake Balaton (drainage at km 1497) by Hungarian fishery biologists. A first attempt was made with *P. intermedia* in 1955 and a second one with both species in 1964 (*P. lacustris* indicated as *P. kowalewsky* in Băcescu, 1966). Despite long-term monitoring by the biological station at Tihany (e.g., Ponyi *et al.*, 1971) and the detailed study of Muskó & Leitold (2003) on the distribution of malacostracans in Lake Balaton, no *Paramysis* species were ever reported from this lake. Own sampling in 1983, 1997, 1998 and 2005 always yielded *Limnomysis benedeni*, but no *Paramysis* species. The same result was achieved by three hand net samples taken by L. Forró and H. Nesemann at different stations in Lake Balaton in 1990-1991 (Nesemann *et al.*, 1995).

Both species did not survive the first winter after introduction into the Rybinsk reservoir in the most northern reach of the Volga, 2900 km from the Caspian Lake (Slynko *et al.*, 2002). By contrast, introduction of *P. intermedia* into hydropower reservoirs in the middle reach of the Volga in 1957-1966 was successful (Borodich & Havlena, 1973). Extensive successful introductions of *P. lacustris* and *P. intermedia* were carried out in vast areas of the Ukraine, Crimea Peninsula, Uzbekistan, Kazakhstan and Kirgizstan, particularly to the lakes Aral, Balkhash and Issyk-Kul (Mordukhai-Boltovskoi, 1979; Komarova, 1991; Grigorovich *et al.*, 2002; Aladin *et al.*, 2003). Following release into water reservoirs and lakes draining into the Baltic Sea, *P. lacustris* established itself in a great number of waters of Lithuania (Arbaciauskas, 2002). It was also introduced in reservoirs of the Western Dvina (= Daugava), from where it subsequently spread into coastal lakes of Latvia (Gasiunas, 1972); additional introductions include the Volkhov reservoir that drains into Lake Lagoda (Zhuravel, 1969). A secondary spread, subsequent to introduction, was reported for *P. lacustris* populations in the Neman, Western Dvina, Dnieper and Volga Rivers. In the 1960s this species appeared in the Gulf of Finland (Jansson, 1994; not shown in Fig. 3 due to missing details on location).

MODES AND FACTORS OF DISPERSION: Van der Velde *et al.* (2000) listed the success factors for crustacean invaders, most of which were also relevant for mysids. Unintentional introductions of mysids were mainly referred to navigation, particularly transport in ballast water, in cooling-water filters and on the outside wall of ships; construction of waterways and inadvertent stocking were also reported to be of major importance.

Jazdzewski & Konopacka (2002) argued that the massive invasion of Ponto-Caspian species in central to western Europe may have been facilitated by the increasing ionic content in large rivers caused by industrial und agricultural pollution during recent decades. This may be relevant for the invasions by the more (*Hemimysis anomala*) or less (*Limnomysis benedeni*) halophilic mysids, but needs to be differentiated for the Rhine and Danube Rivers: after several decades of increase, the ionic content distinctly decreased in these river systems over the last 1-2 decades (Weilguni & Humpesch, 1999; Van der Velde *et al.*, 2000). According to Kelleher *et al.* (2000) and Van der Velde *et al.* (2000), the improved water quality of the Rhine may have facilitated the establishment of certain invaders. This is supported by own observations in the Danube, where the appearance of *H. anomala* in 1998 and *Katamysis warpachowskyi* in 2001 preceded the re-establishment of the stenoecious, indigenous snail *Theodoxus danubialis* (C. Pfeiffer, 1828) in 2004 (9 Sept., six snails sampled with drift net (!), together with *L. benedeni*; at river-km 1933 in Vienna), after four decades without positive records of the snail in the Austrian reach of the main river. In the 1930s this snail was common along river banks in Vienna, became rare in the 1950s, and was declared as already extinct for Austria by Reischütz (1981), but has persisted in a relict population in the Leitha River, a tributary of the Danube (Frank, 1982). When sampling for neozoans in 2005, hundreds of *Theodoxus* were seen on stones and concrete walls along the banks of the Danube in Vienna. The Austrian reach of the Danube has been subject to intensive faunistic studies since the 1930s (e.g., Vornatscher, 1938; Moog *et al.*, 1994), clearly confirming that all currently observed mysid species are neozoans rather than re-established indigenous faunal elements, such as the *Theodoxus* snails.

Simberloff & Von Holle (1999) and Ricciardi (2001) explained part of the success of Ponto-Caspian invaders by "invasional meltdown", i.e. that preceding invasions could facilitate subsequent invasions. Accordingly, the zebra mussel *Dreissena polymorpha* (Pallas, 1771) as a primary invader provided substrate, food and shelter for subsequent invaders. In the case of mysids, such interactions may be complex and require detailed future studies: *K. warpachowskyi* was repeatedly found in accumulations of stones and shells and thus may profit from empty *Dreissena* shells as shelter; adult *H. anomala* are strong predators of small crustaceans and may profit from the mass occurrence of the invasive amphipod *Chelicocorophium curvispinum* (G.O. Sars, 1895) as food in the Rhine and Danube systems. On the other hand, *L. benedeni*, *K. warpachowskyi* and the juveniles of *H. anomala* are mostly micro-herbivores: their food supply may be reduced by strongly enhanced plankton clearance rates (Ojaveer *et al.*, 2002) due to invasions by *D. polymorpha*.

The mysid invaders *H. anomala*, *L. benedeni* and *K. warpachowskyi* have in common that they are euryhaline and often found in great densities in harbours

(Wittmann, 2002). Ports are considered to be distribution hubs of invertebrates (Ricciardi & Rasmussen, 1998). The strong increase of traffic along European waterways during the last decades could partially explain the observed acceleration of mysid invasions.

EFFECTS AT THE ECOSYSTEM LEVEL: Detrimental effects from introductions or invasions of Mysidae species in continental waters have been reported for a number of species, particularly *Hemimysis anomala*, *Mysis diluviana* Audzijonyte & Väinölä, 2005, *M. relicta* Lovén, 1862, *Neomysis mercedis* Holmes, 1896 and *Paramysis lacustris*. Damage at the ecosystem level was mainly related to overgrazing of zooplankton and subsequent effects (Rieman & Falter, 1981; Fürst *et al.*, 1984; Koksvik *et al.*, 1991; Ketelaars *et al.*, 1999; Haskell-Presenter, 2004) and to out-competing of native species by invaders (Arbaciauskas, 2002, 2005; San Francisco Bay Institute, 2004). In particular the top invader *H. anomala* is the focus of great concern due to its high expansion potential in combination with potential mass occurrences and due to its role as a predator of zooplankton. This species is essentially omnivorous with increasing percentage of zooplankton consumption with increasing body size (Borcherding *et al.*, 2006). One important prerequisite for mass occurrences is deeper water, because the photophobic mysids are pelagic during the night and inhabit the dark zone or the bottom during the day, where they are more protected from predation by visually oriented fish.

Limnomysis benedeni and *Katamysis warpachowskyi* are essentially microherbivorous filter feeders with a small portion of their diet composed of invertebrates. This leaves them a more marginal role in the food web as compared to the two *Mysis* species and to *H. anomala*. *L. benedeni* and *K. warpachowskyi* are also more benthic than these species. Accordingly, Wittmann & Ariani (2000) and Wittmann (2002) did not expect strong detrimental effects by *L. benedeni* and *K. warpachowskyi*. No strong impact on the zooplankton community was observed after the invasion of *L. benedeni* in the backwater Alte Donau in Vienna (Wittmann & Ariani, 2000). After a first occurrence in 1993 the population densities of *Limnomysis* peaked in 1996-2000, as revealed by hand net collecting along the shore. This peak was followed by a marked reduction in 2002-05, concurrent with increased water transparency in the course of successful restoration measures.

The above-cited data suggest that mass occurrence is an important prerequisite for potential environmental damage by mysids. The mass occurrences here reported for *H. anomala* and *L. benedeni* were local and/or short-lived. This was not directly observed for the occurrence in drift samples, but mass occurrences would have been short-lived effects of flood events there as well (discussed above).

FUTURE PROSPECTS: Upon first detection of *Limnomysis benedeni* in the French reach of the River Rhine, Wittmann & Ariani (2000) speculated that the range expansion of this species could continue into the system of navigation channels in France, from where the mysid could spread along the Rhône River down to the Mediterranean coast. With the above-presented new records from several navigation channels, the first part of this prediction has become true earlier than expected. If its range expansion continues at the same speed, *Limnomysis* could reach the Mediterranean coast within a few years, with unknown consequences. The indigenous populations of the closely related genus *Diamysis* Czerniavsky, 1882, represented by a number of species in brackish to freshwater bodies all around the coasts of the Mediterranean, could be particularly affected.

If the diffusion of *Hemimysis anomala* along the Rhine system continues, it may enter Lake Constance (Bodensee) and, in the long term, also other deep lakes in Switzerland and neighbouring countries. This could represent a threat to the lake ecosystems in that it leads to overgrazing of zooplankton. Similarly, the Ponto-Caspian gammarid amphipod *Dikerogammarus villosus* (Sowinsky, 1894), a recent invader of Lake Geneva (Bollache, 2004), is expected to spread into other lakes and to seriously threaten the biodiversity in European freshwater ecosystems.

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